REASSESSMENT OF THE TAXONOMIC STATUS OF THE SEA TURTLE GENUS *NATATOR* McCULLOCH, 1908, WITH A REDESCRIPTION OF THE GENUS AND SPECIES

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Summary

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The taxonomic status of the flatback turtle *Chelonia depressa* is reconsidered in terms of electrophoretic and osteological data. While both kinds of data show greatest affinity with *Lepidochelys*, the similarity, in each case, is comparable to that between *Caretta* and *Eretmochelys*. *C. depressa* is dissimilar from *Chelonia mydas*. Because of its distinctiveness, the genus *Natator* is resurrected to accommodate the species *depressa*.

KEY WORDS: Taxonomy, *Natator*, *Chelonia depressa*, osteology, electrophoresis.

Introduction

The taxonomic relationship of sea turtles (Cheloniidae and Dermochelyidae) has been examined using serological and serum electrophoretic methods (Frair 1979, 1982). Zangerl (1980) proposed a phylogeny for the Cheloniidae based on fossil and extant skeletal material. The Australian endemic sea turtle, *Chelonia depressa*, was not included in these studies. The earliest account of the species was supplied by Stokes (1846) when visiting Delambre Island (what we now know to be a large *C. depressa* rookery in Western Australia) on 27 August 1840: "A few turtles were taken, of a different kind from any we had seen before and apparently a cross between the Hawk's Bill and the Green Turtle. . ." The species was described by Garman in 1880 and its taxonomic status has been reviewed on several occasions. Boulenger (1889) placed *C. depressa* in synonomy with *C. mydas* while Baur (1890) considered *depressa* warranted separate generic ranking. McCulloch (1908) erected a new genus and species (*Natator tesselarus*) for an immature specimen which Fry (1913) showed was identical with *depressa*; Fry retained *depressa* and *mydas* as separate species within *Chelonia*. Barbour (1914) showed Garman's 1880 type series to be a composite of *mydas* and *depressa*. Loveridge (1934) thought it "more probable that the type of *depressa* is an aberrent individual which should be referred to the synonomy of *mydas*". As noted by Cogger & Lindner (1969), many workers outside Australia listed *depressa* as conspecific with *Chelonia mydas*. Within Australia, *depressa* was usually recognised as not part of *Chelonia mydas* (Glauert, 1928), although a correct identification was not always made (e.g. *Chelonia japonica*, Worrell 1963; photo of "young loggerhead turtles", Ellis 1937). Williams *et al.* (1967) suggested that *Chelonia depressa* was morphologically so distinct from other *Chelonia* populations that it may be regarded tentatively as a species. The same study, like those before it, suffered from having a small series of preserved museum specimens available for examination. Cogger & Lindner (1969) and Bustard & Limpus (1969), reporting on sympatric nesting by *C. depressa* and *C. mydas*, established *C. depressa* as distinct. Cogger *et al.* (1983) clarified the designation of a lectotype.

The present study examines the relationships of *Chelonia depressa* to four pantropical species of cheloniid turtles which occur in Australia (*Caretta caretta*, *Chelonia mydas*, *Eretmochelys imbricata* and *Lepidochelys olivacea*) using enzyme electrophoresis and skull osteology. The results of these analyses, supplemented by examination of general morphological and behavioural characters, lead to the re-establishment of the genus *Natator* and confirmation of the species *depressa*.

Materials and Methods

Electrophoresis: Muscle tissues for analysis were collected from eastern Australian turtles as follows. Hatchlings were frozen at −20°C in a domestic freezer for return to the laboratory where samples of the pectoral muscle were removed for analysis. Muscle biopsies from the triceps brachii and brachialis inferior muscles of large turtles were taken at their point of capture using "Tru-cut" (Travenol Laboratories) biopsy needles (Gyuris & Limpus 1986). Hatchling *Chelonia depressa* (n = 10) were collected at Mon Repos (24°48'S,

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TABLE 1. *Enzymes examined.*

Protein (EC number)	Abbreviation	Buffer system*	Voltage	Time (min)	Stain reference
Creatine kinase (EC 2.7.3.2)	CK	v	250	120	Richardson 1983
Fumerase (EC 4.2.1.2)	Fum	i	250	40	Richardson *et al.* 1980
Glucose phosphate isomerase (EC 5.3.1.9)	GPI	v	300	90	Richardson *et al.* 1980
Glycerol-3-phosphate dehydrogenase (EC 1.1.1.8)	G-3-PDH	i	250	60	Richardson *et al.* 1980
Lactate dehydrogenase (EC 1.1.1.27)	LDH	vi	250	40	Richardson *et al.* 1980
Malate dehydrogenase (EC 1.1.1.37)	MDH-1	iv	250	60	Richardson *et al.* 1980
Malate dehydrogenase	MDH-2	iv	250	60	Richardson *et al.* 1980
Phosphoglucomutase (EC 2.7.5.1)	PGM	i	250	60	Richardson *et al.* 1980
Phosphoglycerokinase (EC 2.7.2.3)	PGK	iii	250	120	Richardson 1983
Pyruvate kinase (EC 2.7.1.40)	PK	ii	250	60	Richardson 1983

* Buffer systems: i 0.05 M Tris-citrate, pH 7.1; ii 0.05 M Tris-maleate, pH 8.0; iii 0.05 M Tris-citrate, pH 6.8 (+ 1 mM EDTA); iv 0.05 M Tris-citrate, pH 7.0; v 0.05 M Tris-maleate, pH 8.2; vi 0.1 M Tris-maleate, pH 6.5.

152°27'E). Adult and hatchling *C. mydas* (n = 206) were collected at Heron Island (23°26'S, 151°55'E) and adjacent reefs. Adult and hatchling *Caretta caretta* (n = 506) were collected at Mon Repos and adjacent mainland beaches and from Heron Island and adjacent reefs and islands. Immature *E. imbricata* (n = 16) were captured on the coral reefs adjacent to Heron Island. *L. olivacea* (n = 2) were captured at inshore feeding grounds off Cairns (16°55'S, 145°47'E) and Townsville (19°17'S, 146°20'E). All specimens were frozen immediately following collection, transported and stored at −20°C. Approximately 10–30 mg subsamples of the muscle samples were placed in a perspex multi-well tray and 75–100 microlitres of homogenising solution (0.2 mM Cleland's reagent in distilled water) was added to each specimen. Tissues were macerated by grinding within each well. Homogenates were centrifuged in capillary tubes (microhaematocrit tubes, Clay-Adams). Clear supernatants were obtained after breaking away those sections of the capillary tubes containing fibrous material at one end and lipid layer at the other. Individual supernatants were stored in wells of microtiter trays maintained at 0–4°C. All electrophoresis was completed within 48 hr of thawing of the muscle tissues.

Zone electrophoresis was run using cellulose acetate gel supporting medium ("cellogel", Chematron). Constant voltage was delivered to electrophoretic tanks (Shandon Southern) via Pharmacia EPS 500/400 power supplies. Paper wicks of 0.33 mm thickness (Whatman Chromatography paper) were used to ensure an even buffer front. Gels were pretreated prior to sample application according to manufacturer's recommendations. Samples were loaded onto the gels using a draftsman's ink pen. Enzymes studied are listed together with their optimum running conditions and staining methods in Table 1. Enzyme nomenclature used throughout is that recommended by the Commission on Biochemical Nomenclature (1972). Where several isozymes were detected, they were numbered in order of decreasing electrophoretic mobility. Initially a subsample of approximately 60 specimens was screened for allozyme variation in both *Chelonia mydas* and *Caretta caretta*. Only loci that were found to be polymorphic were then screened in every specimen of the species. All *depressa*, *E. imbricata* and *L. olivacea* were examined for 19, 15 and 12 enzyme systems respectively. Nei's genetic distances (D) and their corresponding standard errors were calculated (Nei 1978). A dendrogram was constructed using the

TABLE 2. *Comparison of selected osteological characters of the skulls of the members of the Cheloniidae.*

Species (sample size)	*Chelonia mydas* (26)	*Natator depressa* (8)	*Lepidochelys olivacea* (3)	*Eretmochelys imbricata* (10)	*Caretta caretta* (13)
external pterygoid process	nil	large horizontal	large horizontal	vertical	vertical
pterygoid muscle groove	large distinct	slight	slight	nil	nil
pterygoid extends posteriorly beyond the opening of the foramen posterius canalis carotici interni	yes	no	no	no	no
maxillary lingual ridge	present	present	nil	present	nil
prefrontal and postorbital do not meet (frontal forms part of the orbit)	yes	no	no	yes	no
fenestra ovalis divided by a septum, or nearly so	no	yes	no	no	yes
development of tuberculae basioccipital	low	prominant	low	medium	low
number of channels of posterior of squamosal	2	1	2	2	1
shape of posterior margin of basisphenoid	shelf	vertical wall	vertical wall	vertical wall	vertical wall
Vagus X enclosed or partly enclosed by exoccipital	no	yes	no	no	no
Vomer contacts premaxillary	yes	yes	yes	yes	no
descending process of the prefrontal connects with the palatine	yes	no	no	no	no
pterygoid meets jugal	yes	yes	no	no	no

unweighed pair-group arithmetic average cluster analysis (UPGMA) method (Ferguson, 1980).

Skull Osteology: Skulls of each species of turtle were examined for a suite of morphological characters (Table 2). Terminology and definitions follow Gaffney (1979). Skeletal material examined included specimens gathered during field studies by the Queensland National Parks and Wildlife Service (QNPWS) and specimens held in the collections of the Queensland Museum, Brisbane (QM), Australian Museum, Sydney (AM) and Museum of Comparative Zoology, Harvard (MCZ) as follows: AM R28486, female, Port Essington, 27 March 1967. QM J3848, Queensland, collected pre 1923; J4058, Mackay, collected pre April 1924. QNPWS: X28144, unsexed adult, Cape Hillsborough, 1982; X33703, adult female, Facing Island, January 1970; X33704, adult female, Peak Island, December 1981. Two unnumbered hatchlings from Mon Repos, January 1982. MCZ4473 (Lectotype), "Northern Australia". A detailed description of the osteology of *depressa* is in preparation (J. Hendrickson pers. comm.).

Supplementary Information: Photographs of the specimens of Garman's (1880) type series in the Museum of Comparative Zoology (MCZ), Boston, were examined. Information and data on the general biology, behaviour and external morphology of adults and their eggs and hatchlings were extracted

TABLE 3. *Similarity matrix of Nei's genetic identity values.*

	Natator depressa	*Lepidochelys olivacea*	*Caretta caretta*	*Eretmochelys imbricata*
Chelonia mydas	0.52 (0.38)	0.70 (0.40)	1.01 (0.43)	0.70 (0.40)
Natator depressa		0.22 (0.35)	0.56 (0.38)	0.36 (0.37)
Lepidochelys olivacea			0.76 (0.40)	0.51 (0.38)
Caretta caretta				0.40 (0.36)

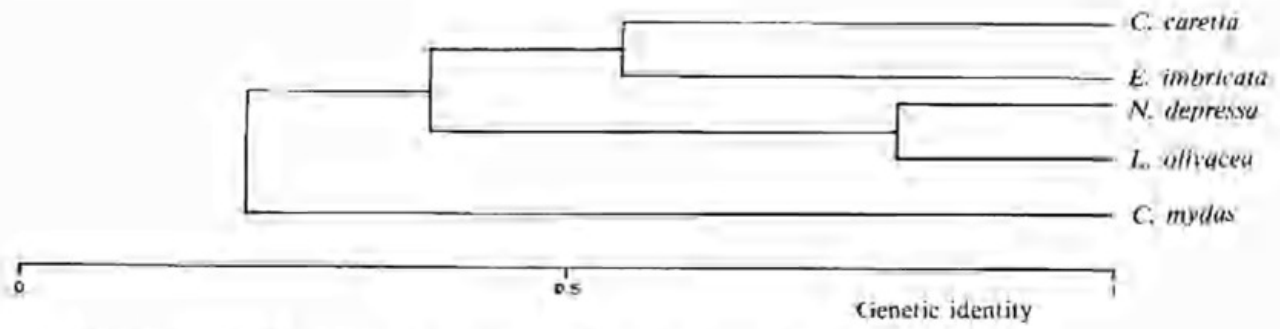

Fig. 1. Dendrogram of cheloniid turtle relationships based on electrophoretic data (Table 3).

from the literature: Coburg Peninsula and other areas of the Northern Territory (Fry 1913; Cogger & Lindner 1969); Crab Island (Limpus *et al.* 1983); south east Queensland (Limpus 1971, Limpus *et al.* 1981).

Results

Electrophoresis

A survey of 27 presumptive loci, coding for protein products in *Chelonia mydas* and *Caretta caretta* revealed low levels of genetic variation (Gyuris & Limpus 1988). Paucity of electrophoretic variation also characterised *depressa* and *E. imbricata*. Ten loci could be used without ambiguity from the five species of sea turtles examined (Table 1) and the results are summarised in Table 3 and Fig. 1. The greatest similarity was found between *depressa* and *L. olivacea*. Similarity between *depressa* and *Chelonia mydas* was less than that between *Caretta caretta* and *E. imbricata*.

Skull osteology

Gaffney (1979) provides an annotated review of the primary literature concerning the skulls of marine turtles and presents illustrations of all recognised cheloniid species except *depressa*. Hay (1908), Kesteven (1911), and Carr (1952) provide additional illustrations. Fry (1913) described some aspects of the cranial osteology of *depressa* based on observations of a single immature skull and provided a comparison of specific features of the skulls of *depressa* and *mydas* based on 1 and 7 specimens respectively. Those notes are re-presented with new information in Table 4. The description and illustration of the pterygoid of *depressa* given by Fry (1913, Fig. 49F) are incorrect because the external pterygoid processes were omitted. The correct position and shape of the external pterygoid process are illustrated in Fig. 2A. The external pterygoid process projects laterally from the pterygoid and terminates with a slight twist with an upward inflection and is characteristic of all *depressa* skulls examined. The skull from which Fry prepared his description (Fry 1913) (specimen No. 7) cannot be located for re-examination (H. G. Cogger pers. comm.). The reason for the omission cannot be determined. The details of the descriptions of the skulls given by Fry indicate that if the process had been present he would have described it. The type specimen for *N. tessellatus* (AM R4158) also cannot be located for re-examination (H. G. Cogger pers. comm.). Attempts to observe the pterygoid bones of the lectotype of *depressa* (MCZ 4473) using X-rays were unsuccessful. This was because the head of this specimen had been filled with plaster of paris when originally mounted.

The skulls of *depressa* and *Lepidochelys olivacea* and *L. kempii* have very similar pterygoid bones which differ markedly from those of *Chelonia mydas* (Fig. 2B) and the remaining cheloniid turtles. A comparison of selected osteological characters of the skulls of members of the Cheloniidae (Table 2) shows *depressa* differs from *Chelonia mydas* in many characters. Of the 13 characters considered, *depressa* and *mydas* differed by ten features; whereas, *depressa* and *L. olivacea* differed by six. *depressa* differed from *C. caretta* and *E. imbricata* by seven and eight features respectively.

TABLE 4. *Detailed comparison of selected osteological characters of the skulls of* Chelonia mydas *and* Natator depressa.

Chelonia mydas	*Natator depressa*
Frontal forms part of orbit	Frontal not forming part of orbit
Prefrontal and post orbital do not meet	Prefrontal and post orbital meet
Opening of foramen posterius canalis carotici interni within pterygoid; not contiguous with other bones	Opening of foramen posterius canalis carotici interni not within pterygoid; contiguous with exoccipital and basioccipital
Exoccipital not separating fenestra ovalis with a septum	Exoccipital separates fenestra ovalis with septum to form (or nearly form) tube
Processus pterygoideus externus wide and only bulges into fossa temporalis inferior without distinct dorsal inflection	Processus pterygoideus externus narrow extending into fossa temporalis inferior with distinct terminal dorsal inflection
Basioccipital with low rounded tuberculae; basioccipital protruding on either side of wide trough	Basioccipital with prominent tuberculae; basioccipital forming vertical walls of narrow trough
Foramen nervi hypoglossi situated in recess of exoccipital	Foramen nervi hypoglossi situated on flat area of exoccipital
Posterior of squamosal with two steep walled channels	Posterior of squamosal with single wide channel
Interorbital space, at outer angle of frontal, one-third of greatest width of skull	Interorbital space, at outer angle of frontal, two-thirds of greatest width of skull
Parieto-squamosal suture always quite distinct, to 3.8 cm in length in adults	Parieto-squamosal suture extremely small
Fronto-parietal suture strongly arched	Fronto-parietal suture transverse
Length of fronto-parietal suture two-thirds to three-quarters greatest width of frontals	Length of fronto-parietal suture equals greatest width of frontals
Pterygoids deeply constricted on each side by oblique pterygo-mandibular sulcus	Pterygoids not constricted by deep pterygomandibular sulcus on each side
Basisphenoidal ridge angled posteriorly to form shelf	Basisphenoidal ridge presents vertical wall at posterior face

Based on these characters, the skull of *depressa* is least similar to *mydas* and most similar to *L. olivacea*. Based on skull characteristics, *depressa* and *mydas* should not be considered congeneric.

Supplementary information

depressa is a carnivorous turtle that feeds principally on benthic animals in soft bottomed communities. It also eats jellyfish. Its carnivory contrasts with the herbivory of the green turtle. *depressa* feeds more on soft-bodied prey (soft-corals, sea-pens) rather than on prey with thick exoskeletons as is eaten by *Lepidochelys* and *Caretta*.

depressa at all sizes except hatchlings and early post hatchlings has a smooth low domed carapace which is distinctly reflexed dorsally at the lateral margins (Bustard & Limpus 1969; Limpus 1971). In cross section the carapace is bow-shaped; in other cheloniid species the carapace is much higher domed and not reflexed on the lateral margin. Hatchling and early post-hatchling *depressa* are not as high domed as the hatchlings of other species but do not have the dorsally reflexed marginal rim. Relative to this characteristic, within the Cheloniidae, *Lepidochelys* with its wide flat marginal rim to the carapace shows the greatest similarity to *depressa*.

The integument of the carapace of *depressa* with a CCL greater than approximately 16 cm is a soft, thinly keratinised skin rather than a series of hard, keratinised scutes. To the touch, it is very similar to the carapacial skin of *Dermochelys coriacea*. Following death and decomposition, there are no large keratinised scutes which can be peeled from the carapace, as occurs with the other cheloniids. Because of the reduced epidermal keratinisation of the carapace, the scutes which are so prominent on

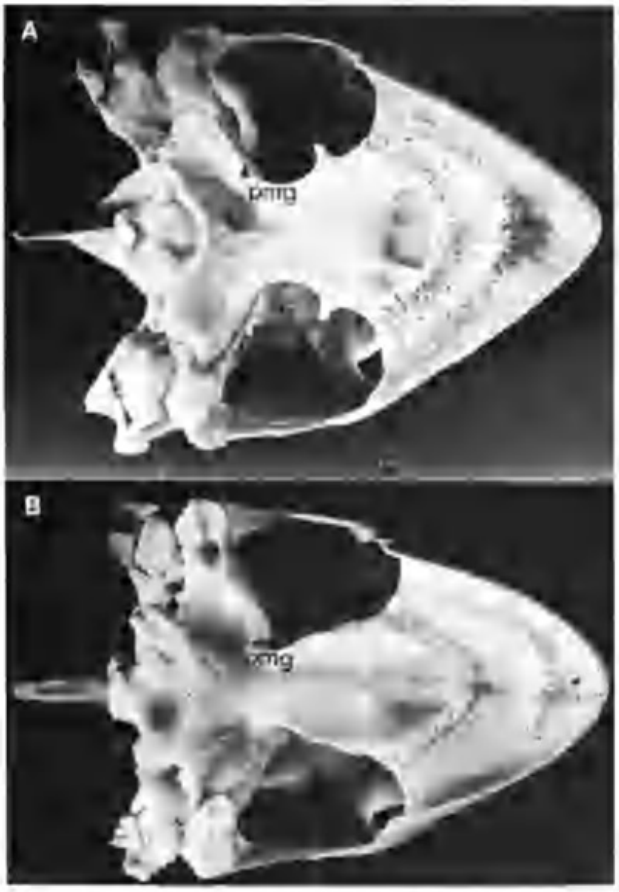

Fig. 2. Ventral view of sea turtle skulls. epp = external pterygoid process. pmg = pterygoid muscle groove. A. *Natator depressa*, adult female (QNPWS X33704). Note the prominent external pterygoid process and poorly developed pterygoid muscle groove. B. *Chelonia mydas*. Note the absence of the external pterygoid process and the well developed pterygoid muscle groove.

the hatchlings are difficult to delineate in the adult. The scutes of the hatchlings are usually strongly pitted and form areolae-like structures as each scute area increases during growth. The areolae are shed to produce the smooth skin like surface of the carapace (CCL between 10 and 16 cm). Within the Cheloniidae, post hatchling *Lepidochelys* also have limited keratinization of carapacial scutes.

Only hatchling *depressa* and *C. mydas* are white ventrally, although the ventral surface of some hatchlings of the other species of Cheloniidae can be light coloured (yellowish instead of brown). In contrast the adults of all species of the family are light coloured (white, cream, or yellow) ventrally. Only in *depressa* and *C. mydas* does a distinct white band outline the margin of the carapace and the flippers. Dorsally *depressa* hatchlings are the most distinctively coloured of all the sea turtles (Limpus 1971).

The gait of hatchling *depressa* on the beach is the typical alternating gait used by all hatchling Cheloniidae. Adult *depressa* move by pushing with all four flippers together in a manner similar to that of *C. mydas* and *D. coriacea* (Limpus 1971). The short front flippers of *depressa* result in a track with less of the front flipper print remaining outside the hind flipper prints than occurs with *C. mydas*.

During egg laying, *depressa* leaves one hind flipper within and pressed against the wall of the egg chamber while the other hind flipper is placed flat on the sand surface to partly cover the opening of the egg chamber (Bustard *et al.* 1975). This posture resembles that of *C. mydas* and *D. coriacea*. In contrast *Caretta*, *Eretmochelys* and *Lepidochelys* have both hind flippers removed from the egg chamber and flat on the sand behind the egg chamber while laying.

The eggs of *depressa* are characteristic and distinctive from those of other species of Cheloniidae. The mean egg diameter measures greater than 4.65 cm and the mean clutch count is approximately 50 (Cogger & Lindner 1969; Limpus, 1971; Limpus *et al.* 1983). The eggs of *depressa* are large and of similar size to those of *D. coriacea* but clutches can be distinguished from the latter because *D. coriacea* clutches always include large numbers of small irregular shaped yolkless eggs (Limpus *et al.* 1984), while yolkless eggs rarely occur in *depressa* clutches and then only in small numbers (Limpus 1971; Limpus *et al.* 1983). Hirth (1980) provides a summary of clutch data from non-Australian populations of other species.

The specimen illustrated by Deraniyagala (1971) as a possible *depressa* from Ceylon in no way resembles any *depressa* we have ever seen and its identification is not supported. The Garman (1880) specimen of *depressa* from East Indies has been shown to be a hatchling *Chelonia mydas* from Penang, Malaysia (Barbour 1914). The only record of *depressa* from beyond the Australian Continental shelf is based on photographs of a stuffed immature specimen from off the north coast of Java (photographs made in 1984 by G. Usher were examined by CJL). The species has been recorded breeding only in Australia where it has a wide nesting distribution. Major breeding aggregations can be found at Peak Island, Wild Duck Island and Avoid Island in central eastern Queensland; Deliverace Island and adjacent islands or north western Torres Strait; Crab Island and the Sir Edward Pellew Islands in the Gulf of Carpentaria; Wessel Islands, Greenhill Island and Field Island in the Northern Territory and Delambre Island on the north west shelf of Western Australia. There are numerous other less important nesting locations.

Discussion

Interpretation of the present electrophoretic study is limited because of the small number of loci used

(Nei 1978). However even with that constraint the data still provide useful information. Friar (1982), in reviewing all the available biochemical data based on serum electrophoresis (band-counting method), immuneoelectrophoresis and serology, constructed a tentative dendrogram suggesting possible sea turtle relationships. The present study corroborates Friar's model and extends it by examining the taxonomic status of *depressa*. On the basis of the electrophoretic data it would appear inconsistent to continue viewing *depressa* and *mydas* as congeneric.

Most taxonomic revisions of *depressa* have been based on examination of a small number of museum specimens. Several unusual characters of the species, especially the thinly keratinised scutes and the upwardly reflexed lateral marginal rim of the carapace, have in the past led to the idea that the lectotype of *depressa* (Fig. 3) was possibly an aberrent specimen (Loveridge 1934; Williams *et al.* 1967). This specimen is not aberrent but is a good representative of the adult *depressa* which can be seen on any of its numerous rookeries in tropical Australia. If there is anything unusual about the lectotype, it is in terms of the way the flippers have been prepared for display.

Baur (1890) commented that clarification of the generic status of the flatback turtle had to wait "until the skull of this species is known. . ." This has been rectified. Both the electrophoretic and osteological characteristics of *depressa* provide a clear separation of it from *Chelonia* at the generic level.

Past studies have noted similarities between *depressa* and *Lepidochelys* (Baur 1890; Williams *et al.* 1967). The first *depressa* skulls registered in the collection of the Queensland Museum were assigned to *Caretta caretta* after being identified as *Caretta remivaga* (= *Lepidochelys olivacea*; QM J3848) and *Colpochelys kempii* (= *L. kempii*; QM J4058) respectively. The present study has identified many common characters shared by *depressa* and *Lepidochelys*. However this similarity is comparable to the degree of similarity that exists between *Caretta* and *Eretmochelys* and between *Caretta* and *Lepidochelys*. Given the common acceptance of the generic discreteness of these latter genera, *depressa* must also be recognised at the generic level.

These data warrant resurrecting the genus *Natator* to accommodate the species *depressa*.

Genus *Natator* McCulloch

Natator McCulloch, 1908, pp. 126–8.

Type species: *N. depressa* (Garman, 1880).

Diagnosis: Because of the confused history of the nomenclature, the genus *Natator* is redefined based on the original descriptions by McCulloch (1908) and Garman (1880), revisions by Fry (1913) and Williams *et al.* (1967) and descriptions of the morphology from the *N. depressa* nesting populations at Coburg Peninsula (Cogger & Lindner 1969), Mon Repos (Limpus 1971) and Crab Island (Limpus *et al.* 1983) and our more recent unpublished observations.

Body broad, depressed, subelliptical, broadest near or behind the middle. In larger specimens, carapace flattened over the second to the fourth vertebral scutes and with lateral marginal rim reflexed upwards. Head and carapace covered with non-imbricate keratinised scutes, each with distinct symmetrical areolae in the young. Areolae shed before carapace length of approximately 16 cm. In adults, carapace scutes thinly keratinised, indistinct with waxy feel. Usual scute pattern as follows. Carapace: nuchal shield undivided; five vertebrals; four pairs of costals; twelve pairs of marginals. Plastron: thirteen scutes, in two series of six each, preceded by small but well developed triangular intergular. Inframarginals: four on each bridge, no

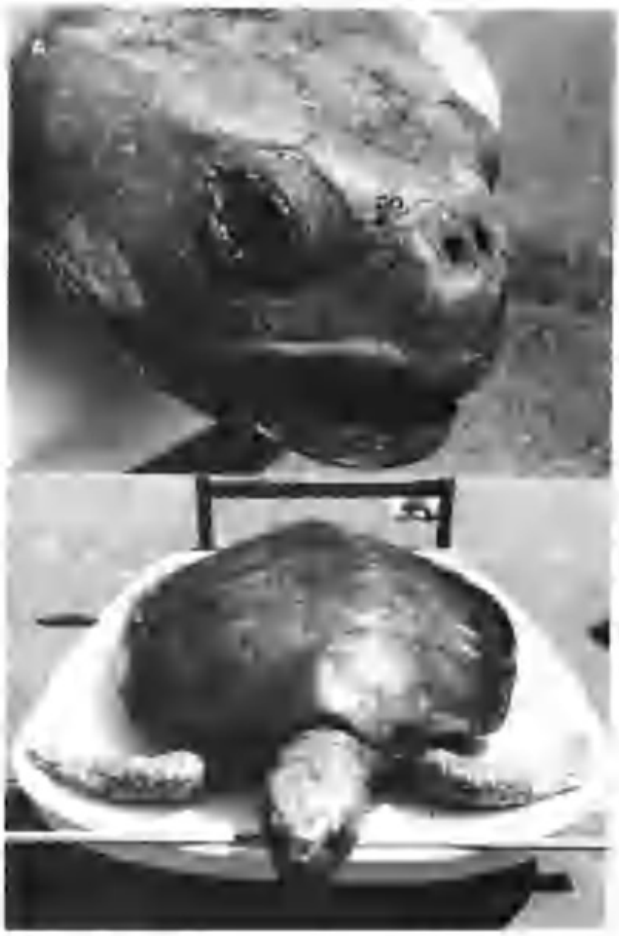

Fig. 3. *Natator depressa* lectotype (MCZ 4473). A. Head showing distinct preoccular scute (po). B. Whole mount showing flattened carapace with reflexed lateral marginal rim and indistinct scutes. Ruler = 1 m.

inframarginal pores. Head: one pair large prefrontals; one pair preoculars lying between prefrontals and upper jaw sheath; frontal in contact with prefrontals and pair of large supraoculars; parietal shield very large; post-parietal in odd numbered series symmetrically arranged behind post parietal (if even numbered array occurs, usually assymmetrically arranged); three post-oculars lying posterior and postero-ventral to each eye, lowest large. Colour: Hatchlings, in life gray dorsally with each scute outlined in black; ventrally white; posterior margin of carapace and flippers outlined in white; iris blue. Adults, in life dorsally olive-gray; ventrally white; iris brown. Limbs: paddle-shaped (= flippers), each with two claws in young (more distal claw becoming less obvious in larger turtles); distal half of forelimb with single rows of enlarged scales extending along phalanges separated by areas of smaller irregular scales or wrinkled skin. Head larger and broader than that of *C. mydas*, broad posteriorly, convex on occiput, flattened between and compressed in front of eyes. Upper jaw not serrated, outline nearly straight, with notch at symphysis almost obliterated, vertically grooved on inner face. Lower jaw serrated (not obvious in hatchlings), bearing sharp recurved prominence on the symphysis. Single choanal spine at each internal naris.

The skull of *Natator* has the following characteristics (Table 3, 4). Frontal not forming part of orbit; prefrontal and post orbital meet. Processus pterygoideus externus narrow extending into fossa temporalis inferior with distinct terminal inflection. Pterygoids not constricted by deep pterygo-mandibular sulcus on each side. Pterygoid not extending posteriorly beyond opening of foramen posterius canalis carotici interni. Fenestra ovalis divided by septum (or nearly divided). Tuberculae basioccipital prominant. Fenestra for vagus X enclosed or partly enclosed by exoccipital. Descending process of prefrontal not connecting with palatine; pterygoid meets jugal.

Natator depressa (Garman) New Comb.

Chelonia depressa: Garman, 1880, Bull. Mus. Comp. Zool. 6, p. 124 (in part); Baur 1890, Amer. Nat. 24, p. 487; Fry 1913, Rec. Aust. Mus. 10, p. 159; Cogger & Lindner 1969, Aust. Zool. 15, p. 154; Bustard & Limpus 1969, Herpetologica, 25, p. 29; Cogger *et al.* 1983, Zoological Catalogue of Australia. Vol. 1. Amphibia and Reptiles, p. 69.

Chelonia japonica: Worrell, 1963, Reptiles of Australia, p. 10.

Chelonia mydas: Boulenger, 1889, Catalogue of the Chelonians, Rhynchocephalians and Crocodiles in the British Museum (Natural History), p. 182; Loveridge 1934, Bull. Mus. Comp. Zool. 77, p. 261.

Natator tessellatus: McCulloch, 1908, Rec. Aust. Mus. 7, p. 126.

Lectotype: MCZ 4473 from northern Australia (possibly purchased in Torres Strait, Barbour 1914) (Cogger *et al.* 1983). Adult sized, probably a female.

Diagnosis: As for the genus.

Geographical distribution: Feeding grounds occur within the warm temperate and tropical waters of the Australian continental shelf, including southern New Guinea waters and along the north coast of Java. Only known to breed in Australia.

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FLINDERS/MOUNT LOFTY RANGES, SOUTH AUSTRALIA THEIR UPLIFT, EROSION, AND RELATIONSHIP TO CRUSTAL STRUCTURE

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Summary

The Flinders/Mount Lofty Ranges are low, elongate highlands. The amount of denudation, the present earthquake activity, and the age of the sediments in the region, are consistent with uplift starting in the Palaeocene or earlier, with uplift and erosion continuing to the present. Seismic, gravity and heat flow observations are consistent with the crustal load of the ranges being supported in regional isostatic compensation by a relatively strong lithosphere, the ranges not having a crustal root, and denudation not being followed by a similar amount of isostatic rebound. The axis of the ranges is coincident with an elongate gravity anomaly high, that may be due to high density in the underlying basement. The ranges probably represent reactivation of the crustal structure causing this gravity anomaly.

KEY WORDS: Flinders Ranges, Mt Lofty Ranges, geomorphology, gravity anomalies, magnetic anomalies, seismic, Adelaide Orogen.